1 Stand history is more important than climate in controlling red maple (*Acer rubrum* L.)
2 growth at its northern distribution limit in western Quebec, Canada

3 Yun Zhang[1*], Yves Bergeron[1], Xiu-Hai Zhao[2], Igor Drobyshev[1,3]

* Author′s current working place

National Plateau Wetlands Research Center, Southwest Forestry University, Kunming, 650224, P. R China.

Y.Z. zhangyuncool@163.com

1 Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue (UQAT), 445 boul. de l'Université, Rouyn-Noranda, Québec, J9X 5E4, Canada.

Phone: YZ +1-819-762-0971 ex. 4370/ID +1-819-762-0971 ex. 2057/YB +1-819-762-0971 ex. 2347/Fax: +1-819-797-4727

Y.Z. Yun.Zhang@uqat.ca / I.D. Igor.Drobyshev@uqat.ca / Y.B. Yves.Bergeron@uqat.ca

2 Key Laboratory for Forest Resources & Ecosystem Processes of Beijing, Beijing Forestry University, 100083, P. R. China.

Phone: XHZ +86-10-62336082 / Fax: +86-10-62338197

X.H.Z bfuz@163.com

3 Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre, P.O. Box 49, SE-230 53 Alnarp, Sweden / Igor.Drobyshev@slu.se

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5 Igor Drobyshev is the corresponding author: Igor.Drobyshev@uqat.ca

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Abstract

Aims We examined growth of red maple (*Acer rubrum* L.) to evaluate environmental controls of its northern distributional limit in Eastern North America and its potential response to future climate change.

Methods We collected growth data from nine sites located along a 300 km transect (47-49° N), which included frontier population of red maple and covered three bioclimatic domains in western Quebec. We analyzed three growth variables: growth rates during the first 30 years of maple lifespan, cumulative basal area increment (BAI) over the most recent decade (2000-2009), and annual growth rate over the whole tree lifespan ranging from 58 to 112 years. We also examined growth sensitivity to climate by using response function analysis.

Important findings Three different proxies of maple growth (initial growth rate, basal area increment during 2000-2009, and mean diameter growth rate) indicated a better growth with an increase in latitude. We speculate that stand history effectively overrode the direct effects of colder climate on maple growth along the S-N gradient. Regeneration of maple in the southern sites likely occurred in canopy gaps, whereas in the north it was contingent upon large disturbances such as stand-replacing fires, which apparently provided more favorable light environment for maple growth than canopy gaps. The annual growth variability, which reflects effects of annual weather on growth and is largely independent from the absolute growth rate, was significantly affected by monthly climate, suggesting a positive effect of higher summer temperature in the northern part of the transect (48-49° N) and a negative effect of summer drought in the south (47-48° N).

In the future, the natural and human disturbance regimes will be dominant controls of the

biomass productivity of red maple at the northern limit of its present distribution range. Direct effects of climate on maple growth would likely be less important in this context, and will likely entail negative effect of increased summer drought in the southern part of the study area and positive effects of increased temperatures in the north.

Key words: biomass productivity, climate change, dendrochronology, ecotone, hardwoods, species migration

INTRODUCTION

Climate influences forest communities by affecting species phenology, growth, and the outcomes of competitive interactions among plants (Hansen *et al.* 2001; Richardson *et al.* 2006; Tylianakis *et al.* 2008). Over the 20th century, annual mean temperature and annual total precipitation in eastern Canada have increased by 0.5-1.5 °C and 5-35%, respectively (Zhang *et al.* 2000). Temperature is expected to increase by an additional 1.5 to 4.5 °C by 2050, accompanied by 10 to 25% increases in the amount of precipitation (Boer *et al.* 2000; Plummer *et al.* 2006). Such changes in climate may have major impacts on tree growth and distribution by affecting plant physiology (Way and Oren 2010), tree sensitivity to environmental variability (Allen *et al.* 2010), and natural disturbance regimes (Bergeron *et al.* 2010). Growth responses to these changes would likely be species-specific (Ashraf *et al.* 2013).

The performance of species at their distributional limits may give clues to understand their responses to long-term climate variability (Wilmking *et al*. 2004; Zhang and Hebda 2004; Griesbauer and Green 2010; Lv and Zhang 2012; Drobyshev *et al*. 2014). Temperature is a crucial factor for tree growth at northern latitudinal and upper altitudinal limits (Fritts 1976; Makinen *et al*. 2002; Frank and Esper 2005). Climate warming has induced a northward or an upward shift of many species at their distributional limits in different temperate biomes (Kullman 1993; Suarez *et al*. 1999; Wilmking *et al*. 2004; Pederson *et al*. 2004; Griesbauer and Green 2010). In eastern North America, temperate hardwood species are expected to migrate further north under warmer climate conditions (Goldblum and Rigg 2005; McKenney *et al*. 2007; Berteaux *et al*. 2010; Terrier *et al*. 2013).

Competition may be another factor that influences species distributional limits (Gavin and Hu 2006; Ettinger and HilleRisLambers 2013). Competition may restrict species ranges by excluding species from potentially suitable habitats (Armas *et al.* 2009), and may also enhance negative effects of sub-optimal climate conditions on tree growth (Scheller and Mladenoff 2008). Therefore, a consideration of competitive interactions between species, together with a detailed analysis of climate-growth relationships, would increase realism in modeling potential shifts in species distributions (Davis *et al.* 1998; Guo *et al.* 2013).

Studies of the long-term forest dynamics have demonstrated that distribution ranges of hardwood species are closely linked to regional climate (Davis 1981; MacDonald 1993). For example, fossil pollen data have indicated that red maple (*Acer rubrum* L.) experienced a northward expansion in North America during the warmer period of the early to middle Holocene (from 11 000 to 7 000 years BP, Delcourt and Delcourt 1987). Dendrochronological methods have a potential to provide high resolution data to help disentangle climate-growth relationships, however there were few dendroclimatological studies on hardwood species at their northern distributional limits in eastern Canada (Tardif and Bergeron 1993; Tardif *et al.* 2006), most of such studies being focused on coniferous species (Drobyshev *et al.* 2010, 2013; Nishimura and Laroque 2011; Genries *et al.* 2012).

Red maple is one of the most widespread broadleaf trees in eastern North America, which also marks the border between boreal and temperate biomes in eastern Canada (Walters and Yawney 1990). In western Quebec, red maple reaches its northern distributional limit around 48º N, where its frontier populations occupy south-facing hill slopes (James and

Courtin 1985; Tremblay *et al.* 2002) and coexist with other deciduous and coniferous species, forming mixedwoods. Spring frost is an important factor affecting red maple sexual regeneration in this region, with waves of maple recruitment being associated with periods of low spring frost frequency (Tremblay *et al.* 2002). However, climate effects on the growth of adult trees, which may be another factor controlling the northern distribution limit of red maple, are poorly understood. Furthermore, presence of abundant regeneration of red maple on recently disturbed sites in this region suggests importance of stand history affecting its recruitment and canopy abundance.

In this study, we examined biomass accumulation rates and growth sensitivity of red maple to annual weather along a 300 km-long latitudinal gradient (47-49º N) stretching from the southern mixed forest to the frontier maple populations in eastern Canada. We put forward two hypotheses: (1) biomass accumulation rate declines with increasing latitude, and (2) annual growth sensitivity to temperature increases with latitude while sensitivity to precipitation decreases with latitude. Both hypotheses assumed that growth was increasingly limited by temperature towards the north, reflecting a trend towards colder conditions and a shorter growing season. We also discussed the growth of red maple under projected climate change and resulting dynamics of its northern limit in eastern North America.

MATERIALS AND METHODS

Study area

Our study was conducted at the Quebec-Ontario border along a latitudinal gradient (47º N to 49º N) extending to the northern limit of red maple distribution (Fig. 1). The study area covered the Abitibi-Témiscamingue region of Quebec, which is dominated by glacial

deposits (Vincent and Hardy 1977; Bouchard *et al.* 2005). Regional topography is generally flat, with small hills reaching elevations of 200 to 400 m a.s.l. Stands with red maple in the canopy are usually found on till deposits or rocky outcrops (Lalonde 1991), with such habitats being more common towards the southern portion of our transect (MRNQ 1998).

Winter climate of the study area is dominated by dry polar air masses, while warm summers bring moist tropical air masses to the region. Average temperature decreases from the southern end of the study transect to its northern end, while the pattern of precipitation is reversed (Table 1). Annual mean temperature is about 1.7 ºC at BEA (the southernmost site) and 0.8 ºC at DUP (the northernmost site). January is the coldest month, with the average mean temperature ranging between -16.9 ºC (BEA) and -18 ºC (DUP). July is the warmest month, with the average mean temperature varying from 17.3 ºC (BEA) to 16.6 ºC (DUP). Total annual precipitation is between 705 mm (BEA) and 746 mm (DUP). Annual mean temperature, collected by on-site temperature sensors (Table 1), varied from 2.43 to 5.01 ºC.

Nine red maple sites were selected across the three bioclimatic domains (Saucier *et al.* 2003), including two sites within the sugar maple (*Acer saccharum* Marsh.) - yellow birch (*Betula alleghaniensis* Britt.) domain in the south (sites BEA and MAR), two sites within the balsam fir (*Abies balsamea* (L.) Mill.) - yellow birch domain in the center of the study area (sites REM and KEK), and five within balsam fir-paper birch (*Betula papyrifera* Marsh.) domain in the north (sites SAB1, SAB2, SAB3, ROQ, and DUP, Fig. 1). An ecological survey at the landscape scale across the three bioclimatic domains has determined that the frequency of red maple decreased from 46% to 11%, moving

northward along our latitudinal gradient (MRNQ 1998).

Soil sampling and analyses

To characterize soil properties, we collected two samples from the soil mineral layer (20-30 cm) at each site, which were combined to form one bulk sample. A portion of the combined sample was air-dried at 20 °C for one week and sieved to pass a 2 mm mesh screen. Soil texture was quantified by the Bouyoucos Hydrometer Method (Sheldrick and Wang 1993, Table S1). A second portion of sample was sieved through a 4 mm screen and oven-dried at 40 °C for 60 hours. We used this portion to determine soil chemical composition (Table S2), including total carbon (C, %), nitrogen (N, %), sulphur (S, %), and phosphorus, together with pH in 0.5 M $CaCl_2$ and cation exchange capacity (CEC). The analytical procedures followed established protocols (Laganière *et al.* 2010) at the Laurentian Forestry Centre of the Canadian Forest Service, Quebec City, Quebec, Canada.

Climate data

Climate data were generated in BioSIM 10.2.2.3, which is a set of spatially explicit bioclimatic models (Régnière 1996). We used BioSim to interpolate climate data that had been obtained from the five weather stations closest to each site, taking into consideration of site latitude, longitude, and elevation. We used data for the period 1964 through 2009, which was the common period across sites and had the highest quality of climate data. Analyzed climate variables included monthly mean temperature and monthly total precipitation from July of the previous year to August of the current year. In addition, we used the Monthly Drought Code (MDC), which was calculated from May to September, to detect the effects of soil moisture on tree growth. MDC is the product of monthly

maximum temperature and total precipitation (Girardin and Wotton 2009) and is considered an indicator of moisture content in the soil deep organic layer (Turner 1972).

To directly assess temperature variation across our study area, we set a temperature sensor (iButton DS1921G, Maxim Electronics, Dallas, Texas) in the center of each site, placing it on the northern side of a tree at 1 m height. The sensors collected data with 3-hour intervals for the period from January the 1st 2011 to December the 31th 2011.

Field sampling and initial data treatment

We selected study sites based on the field surveys of Lalonde (1991) and Tremblay *et al*. (2002). Stand selection was guided by the following criteria: 1) red maple should be present as large (above 10 cm in diameter at breast height) canopy or sub-canopy trees; and 2) red maple should contribute more than 20% in relative species abundance of selected stand. Identifications of stand origin and stand age were based on historical records of forest fires (Lalonde 1991), forest fire database from the Quebec Ministry of Natural Resources and Wildlife, and stand age data available from previous studies (Lalonde 1991; Graignic *et al*. 2013). We assumed that if stand age exceeded the one of the oldest sampled maples, maple recruitment occurred through canopy gaps and not through stand-initiating disturbance.

At each site, we randomly selected 12 to 17 largest maples, measured their diameter at breast height (DBH, 1.3 m) and extracted two cores from each tree at 20 cm above the ground surface. The cores were dried, mounted, and sanded until ring boundaries were clearly visible. Cores were visually cross-dated by using the point year technique (Stokes and Smiley 1968). After cross-dating, ring widths were measured on scanned images in CDendro and CooRecorder software, ver. 7.3 (Larsson 2010). Data quality was

statistically verified using the program COFECHA (Holmes 1983).

Prior to the dendroclimatic analyses, we removed age- and size-related trends in tree ring-width series. The series were detrended with a cubic spline using program ARSTAN (Cook and Peters, 1981). The detrending procedure assumed a 50% frequency response over a 40-year frequency band. We then performed autoregressive modeling on detrended ring-width series to remove temporal autocorrelations and to enhance the common signal. The individual residual series were subsequently averaged together using a biweight robust mean to develop a mean standardized chronology for a site that retained high-frequency variation and which contained no low-frequency trend.

Dendrochronological analyses

Initial growth rates. We developed cambial age chronologies of the first 30 years of tree lifespan to evaluate the initial growth rates and regeneration conditions and compared these rates across domains. To develop cambial age chronologies we calculated mean ring-width (in mm) for each year of growth from year one to year 30, aggregating samples collected within each bioclimatic domain. Since basal area increment (BAI) better represents tree biomass accumulation than does the diameter increment (Pedersen 1998), we converted the data into BAI. To evaluate differences in absolute growth rates among the bioclimatic domains, we fitted BAI cambial chronology by linear regression and tested the differences among b coefficients (regression slopes) using a General Linear Model in SPSS 15.0 (Carpenter *et al*. 2004).

Environmental effects on growth of adult trees. To understand environmental controls of growth for adult trees, we regressed the growth rate against latitude (representing temperature gradient, Table 1), soil pH (representing soil conditions, Table S2), and an

index of competition interactions (Table 1), by using multiple linear regression function *lm* and bootstrapping function boot of the statistical programming language R ver. 3.0.2 (Fox 2000). There was no multicollinearity among the three environmental variables and residuals were normally distributed. To minimize effects of site history, i.e. canopy disturbances and changes in competition levels, on growth dynamics we limited consideration to the most recent 10 years (2000-2009). Similar to the analyses of initial growth, tree-ring data were converted into BAIs. To eliminate age effects on biomass accumulation, we divided BAI of each tree by tree age, and then make an average of adjusted BAI from all trees as site mean BAI.

To calculate competition interactions, we measured DBH of both cored and neighboring trees, and recorded the distances between them. Specifically, we selected the nearest neighbor within each of the four quadrants that were located around the focal maple tree, and which were delimited by the four cardinal directions (i.e., North, South, East, and West). We then used Hegyi's (1974) single tree competition index (*CI*) to quantify the influence of neighboring trees on the focal trees:

$$CI = \sum_{j=1}^{N} \left(\frac{Dj}{Di} \times \frac{1}{DISTij} \right)$$

where *CI* is the competitive load for the focal tree; *Di* is for the focal tree's DBH (cm); *Dj* is for the competitor tree's DBH (cm); *DISTij* is the distance (m) between focal tree i and competitor tree j; and *N* is the number of competitor trees surrounding the focal tree (four in our study). According to this formula, higher *CI* would result from the smaller the size of the focal tree, the larger the size of the competitor, and the lower the local density (i.e., the greater the distance between trees). We averaged *CI* of all of the maple trees from the

same site to estimate site *CI* (Table 1).

Annual growth rate. To further evaluate variability in growth rates along the transect, we calculated mean diameter growth rate of red maple as a ratio between DBH and0 tree age for each site.

Growth sensitivity to annual climate variability We used response function correlations to examine growth sensitivity to climate resolved at monthly scale. A response function is a principal component regression that is used to solve the problem of multicollinearity among climatic predictors (Briffa and Cook 1990; Morzukh and Ruark 1991). Correlation coefficients of the response functions were calculated over the common interval 1965-2009, using the program DENDROCLIM2002 (Biondi and Waikul 2004).

RESULTS

Stand history and soil conditions

The majority of northern sites (ROQ, SAB1, SAB2, SAB3, and KEK) were post-fire stands according to the documentary records of fire events (Lalonde 1991) and data on maximum tree age of red maple in these sites (Table 1). At site DUP the initiation year of the stand and of the sampled maples coincided (Table 1), and absence of recent charcoal suggested a clear-cut event. In southern sites (REM, MAR, and BEA), the maximum age of trees in the forest canopy was higher than that of sampled maples, suggesting that these maples probably regenerated in gaps or under canopy (Table 1).

Soils of all sites showed a high sand content (> 73%, Table S1) and rather acid soil conditions with pH ranging from 3.04 to 4.20 (Supplementary Information Table S2). There was no clear pattern in variation of soil nutrients (i.e. total C, N, and S) along the

latitudinal gradient. Both the northernmost (DUP) and the southernmost (BEA) sites revealed lower nutrient concentrations as compared to more centrally located sites. Cation exchange capacity (CEC) was similar among all the sites (ranging from 17.63 to 23.79), except for the site SAB1 (5.86).

Chronology characteristics

The length of maple residual chronologies ranged from 58 to 112 years, with the oldest chronology dating back to 1897 (Table 1). Chronologies showed high expressed population signals (EPS, ranging from 0.85 to 0.91), while the variation explained by the first principal component (PC) ranged from 29.12 to 49.02%. The chronologies were also similar in terms of their mean sensitivity (MS) varying from 0.24 to 0.31 (Table 1).

Growth rates

Maple growth during the first 30 years of life was significantly higher ($p < 0.001$) in the northernmost balsam fir-paper birch domain compared to the other two domains (Fig. 2). There was no difference between balsam fir-yellow birch and sugar maple-yellow birch domains in terms of the b coefficients representing the increase in growth rate with age during the first 30 years ($p = 0.54$). In all three domains, linear regression fitted the growth patterns well, with R^2 varying between 0.95 and 0.98.

Site average BAI accumulated during 2000-2009 was significantly and positively related to site latitude ($p = 0.032$), while competitive interactions and soil pH did not show significant effects on BAI (Table 2). The average growth rate over the whole tree lifespan was higher in the northern part of transect than in its south (Fig. 3). Trees on the northern sites ROQ exhibited the highest growth rate of 2.97 mm/year (Fig. 3).

Climate-growth relationships

Temperature, precipitation, and soil moisture conditions affected red maple growth (Fig. 4). Temperature in September of the previous year was positively related to maple growth across the whole transect, with significant correlations observed at four sites (ROQ, SAB3, MAR, and BEA). In the northern part of the transect, three out of six sites (ROQ, SAB1, and SAB2) showed significant positive correlations between summer (July) temperatures of the current year and growth, and the growth at all the six northern sites (DUP, ROQ, SAB1, SAB2, SAB3, and KEK) was significantly and positively correlated with precipitation in December of the previous year. In the southern part of transect, summer water deficit appeared to limit the growth, as indicated by significant and negative correlations with July MDC (sites REM and BEA), June temperature (BEA), and August temperature (REM), and by positive correlations with July precipitation (REM and BEA).

DISCUSSION

Growth rate of red maple at its northern distributional limit increased with latitude, which rejected Hypothesis 1 and suggested that decreasing temperatures do not limit biomass accumulation in maple. Initial (first 30 years of tree lifespan) and the most recent (2000-2009) BAI, as well as growth rates averaged over the whole lifespan of the trees were all higher in the northern part of transect, suggesting that stand history was likely to be more important than direct climate variability in controlling biomass accumulation rates. However, annual growth variability was sensitive to temperature in the north of transect and to moisture availability in the south, supporting the idea of increased temperature sensitivity of growth towards the north (hypothesis 2). Below we discuss the

details of these findings and the potential effects of future climate conditions on the northern distributional limit of red maple.

Growth rates along the latitudinal gradient

All growth variables analyzed in this study suggested that growth of red maple increased towards the north (Table 2; Figs. 2 and 3), which falsified our assumption about temperature-driven decline in growth rate with increasing latitude. We believe that differences in stand history (Table 1) may be important in explaining the observed pattern. The sites in the northern balsam fir - paper birch domain regenerated after stand-replacing fires or clear cutting. Maple establishment likely followed such stand-replacing disturbance events, benefiting from high light levels during the early stages of stand development. It is worth mentioning in this context that red maple is one of the most fast growing trees in the northern mixedwood on till soils (Walters and Yawney 1990). In contrast, red maple trees in the more southerly locations (i.e., in sugar maple-yellow birch and balsam fir-yellow birch domains) likely regenerated under the closed canopy and eventually took advantage of canopy gap formation. Overall, this regeneration pathway resulted in both lower light levels and lower growth.

Empirical studies examining northern distributional limit of tree species in Canada have suggested that stand histories (disturbance regimes) may be the main factor controlling species distribution. Low fire frequency and small fire area were suggested to be limiting factor for the northern expansion of Jack pine (*Pinus banksiana* Lamb., Asselin *et al*. 2003). The northern distribution limits of red pine (*Pinus resinosa* Ait.), white oak (*Quercus alba* L.), and yellow birch (*Betula alleghaniensis* Britton) were related to a change in disturbance regime characterized by mixed severity and generally small fires to

severe and large fires along south-north gradient (Flannigan and Bergeron 1998; Sutton *et al*. 2002; Tardif *et al*. 2006; Drobyshev *et al*. 2014).

Local forest management might further modulate maple growth response to climate. An exceptionally high growth rate observed at ROQ (Fig. 3) could be attributed to selective thinning, which was applied to this stand in connection to maple syrup production in the past. A lower stand density leading to decreased competition among trees, appeared therefore to override the effects of sub-optimal climate on maple growth. Red maple has been shown to have strong and positive growth responses to decreases in stand density (Walters and Yawney 1990).

Climate-growth relationships

Red maple growth was generally positively affected by summer temperature in the northern part of transect (sites ROQ, SAB1 and SAB2) and negatively affected by summer moisture in its southern part (sites REM and BEA, Fig.4). Higher temperature likely enhanced photosynthetic rates during the short growing period at the northern sites, thereby favoring tree growth. A southward increase in temperature was accompanied by a decrease in precipitation (Table 1), which likely resulted in a higher water deficit in the south. A recent study conducted in an area of Northern Ontario (De Silva *et al.* 2012) adjacent to our southernmost sites, likewise demonstrated a negative effect of water deficiency on red maple growth. Negative effects of drought stress on red maple growth, shown for the mixed forests of the eastern USA (He *et al*. 2005), might have caused growth declines in red maple over that region (Fekedulegn *et al*. 2003). Negative effects of summer water deficiency on hardwood species have also been observed in sugar maple, which is taxonomically and ecologically related to red maple (Tardif *et al*. 2001),

as well as in other deciduous species of eastern Canada, i.e. trembling aspen (*Populus tremuloides* Michx.), paper birch (Huang *et al*. 2010), and white oak (*Quercus alba* L.; Tardif *et al*. 2006).

Red maple growth in the northern part of transect was positively correlated with precipitation in December of the previous year (Fig. 4). We speculate that deeper snow cover during December would better protect roots from the damaging effects of low temperature. Such relationship has been proposed in many studies of tree growth dynamics at distributional limits. Deep snow cover has been suggested as a factor limiting temperature-related root damage at tree lines both in northern Quebec (Payette *et al*. 1996) and in western Austria (Oberhuber 2004). Positive effects of early winter snow accumulation on tree growth have been reported for Erman's birch (*Betula ermanii* Charm.) at the upper altitudinal limit of subalpine forests in northeastern China and central Japan (Takahashi *et al*. 2005; Yu *et al*. 2007). Negative effects of a reduction in snow cover on growth of sugar maple through damaging roots have been observed in the northern hardwood forest of USA (Comerford *et al*. 2012).

Red maple responded positively to previous September temperature across the entire latitudinal gradient (Fig. 4). Two mechanisms would explain this relationship. First, warmer autumn may lead to a longer growing season for red maple and help increase carbohydrate reserves in roots to be used in the following growing season (Kozlowski and Pallardy 1997; Yu *et al*. 2007). It has been widely reported that root reserves accumulated during the previous year play an important role for early growth of deciduous trees in the following year (Tromp 1983; Cheng and Fuchigami 2002; Hart *et al*. 2012). Secondly, warm autumn could promote root growth by keeping soil warm

(Oberhuber 2004), and increases in root biomass during previous year could facilitate early growth in the following year due to greater root mass allowing better nutrients absorption (Ettl and Peterson 1995).

Future responses of red maple to climate at its northern distributional limit

Our results suggested that effects of future climate on red maple distribution may be realized primarily through climatically-induced changes in the natural disturbance regimes rather than through direct effects of climate on tree growth. The data indicated a strong link between red maple growth rates and the stand histories. The observation apparently reflected plasticity of maple life strategy at its northern distribution limit and, more generally, its ability for recruitment under different disturbance regimes (Lorimer 1984; Hart *et al*. 2012; Duchesne and Prévost 2013). An important element of this strategy appears to be a rapid response to changes in light availability, as it has been shown in the study of red maple response to budworm outbreaks (Duchesne and Prevost 2013), formation of tree fall gaps (Leithead *et al*. 2010; Hart *et al*. 2012), and timber harvesting (Abrams 1998; Duchesne and Ouimet 2008).

A projected increase in the frequency and severity of spruce budworm outbreaks (Gray 2008) and windstorms (Ouranos 2010) in the study region may favor maple colonization of new habitats, particularly - on well and moderately drained parts of landscape. Forest fire may affect northern distributional limit of red maple in different ways depending on variations of fire severity and frequency in future. Red maple can sprout vigorously after fire disturbances (Walters and Yawney 1990). In this study the maple growth rate was higher in stands where maple cohort regenerated immediately after stand-replacing disturbances, as compared to stands with gap-associated regeneration (Fig. 3). This

observation suggested that forest fires may promote maple regeneration. However, high severity fires or those occurring at high frequency likely disfavor maple frontier populations. Thin bark of adult maple trees makes them susceptible to fires of even moderate intensity (Frissell 1973; Walters and Yawney 1990; Abrams 1998), and sever fire may kill roots of maples limiting vegetative regeneration. Frequent fires may reduce the amount of seed resources and lead to low levels of sexual regeneration (Tremblay *et al*. 2002), reducing possibility of colonizing newly available sites across landscape. Severe and/or frequent fires can therefore cause limiting availability of seed sources for recolonization, ultimately leading to a recession of maple northern limit southward.

Considering direct effects of future climate on red maple in western Quebec, it is likely that general warming of the climate would benefit maple recruitment and growth. Climate models predict that temperature will rise by an additional 2.2-3.5 ºC by 2050 over the entire study area, with a greater increase in winter (3.0-4.4 ºC, Ouranos 2010). Models also predict little change in summer precipitation patterns, but a decrease in snow accumulation during the winter (Ouranos 2010). A large increase in the abundance of maple seedlings due to climate warming has been reported at its northern limit in northeastern Ontario (Pinto *et al.* 2008) and eastern Quebec (Duchesne and Ouimet 2008; Duchesne and Prévost 2013), two locations which were geographically close to our study area. These results imply that future warming may also enhance recruitment of red maple in western Quebec. Increasing temperatures have been expected to increase seedling abundance of other tree species at high latitudinal or altitudinal distribution limits (Camarero and Gutiérrez 2004; Gamache and Payette 2005).

In the northern part of the study area (balsam fir - paper birch domain), the warmer

summer may promote radial growth of red maple. During growing period, frontier populations of red maple may also benefit from warmer soil temperatures (Houle *et al.* 2012) and, consequently, increased nitrogen availability (Butler *et al.* 2012), which may be an important factor on sites with increased thickness of soil organic layer. Maple in the southern part of the study area (sugar maple-yellow birch and balsam fir-yellow birch domains) may face more stressful summer conditions in the future. A decrease in summer water availability may have a negative influence in maple growth in the south.

To conclude, future abundance of red maple at the landscape scale in the western Quebec appears to be largely a product of disturbance-mediated effects on its recruitment and growth. Dynamics of future precipitation, which controls levels of fire activity seems to be of immediate importance under generally warmer and longer growing seasons. We believe that better projections of future precipitation should enhance our ability to project future changes in northern distribution limit of red maple in eastern Canada.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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683 Table 1: Stand history, site climatic conditions (1965-2009), and statistical characteristics of red maple residual chronologies from the
684 study sites in western Quebec. Dash indicates no data available. MDC refers to Monthly Drought Code. Competition index refer to
685 estimates of competition conditions of sampled trees only. Annual mean temperature during 2011 refer to on-site measurements.

Sites	DUP	ROQ	SAB1	SAB2	SAB3	KEK	REM	MAR	BEA
Stand history and site location									
Direct records of disturbances year	1950	1880s	1923	1923	1923	1941	-	-	-
Disturbance type	Clear-cut	Fire	Fire	Fire	Fire	Fire	-	-	-
Stand age, maple age	58, 58	112, 112	85, 85	85, 84	85, 84	65, 64	161, 88	110, 83	145, 74
Competition index	0.74	0.39	1.11	0.82	0.98	1.38	0.69	0.7	0.65
Latitude, ^{o}N	48.88	48.55	48.46	48.46	48.46	48.18	47.68	47.36	47.12
Longitude, ^{o}W	79.36	79.41	79.42	79.42	79.42	79.15	79.04	79.28	79.48
Elevation, m	312	330	405	365	350	376	340	293	239
Climatic conditions									
Annual mean temperature, °C	0.8	1.5	1.5	1.5	1.5	1.6	1.5	1.5	1.7
Annual total precipitation, mm	895	907	899	898	898	898	897	887	846
Average summer temperature, °C	15.3	15.9	16.0	16.0	16.0	16.0	15.9	15.9	16.1
Sum of summer precipitation, mm	303	300	292	291	291	288	287	289	272
Average summer MDC	12.6	12.7	12.9	12.9	12.9	13.9	12.5	13.4	14.2
Spring minimum temperature	-2.01	-1.56	-1.53	-1.54	-1.51	-1.17	-1.10	-1.02	-0.98
Spring mean temperature	4.61	5.11	5.17	5.16	5.18	5.33	5.45	5.39	5.50
Spring maximum temperature	11.23	11.33	11.38	11.36	11.37	11.40	11.49	11.53	11.98
Annual mean temperature during 2011	2.43	2.70	2.77	2.74	2.75	3.01	3.48	4.24	5.01
Characteristics of chronologies									
Number of trees (number of radii)	14 (26)	12 (23)	13 (26)	12 (24)	12 (24)	17 (32)	12 (24)	12 (23)	15 (27)
Chronology length	1951-2009	1897-2009	1924-2009	1925-2009	1925-2009	1909-2009	1921-2009	1926-2009	1937-2011
Mean ring width, mm	1.08	1.43	1.07	1.16	1.12	1.05	0.50	0.98	0.86
Mean sensitivity	0.29	0.24	0.27	0.24	0.28	0.28	0.25	0.27	0.31
Period with EPS $\geq$ 0.85	1957-2009	1944-2009	1929-2009	1936-2009	1951-2009	1952-2009	1965-2009	1957-2009	1953-2011

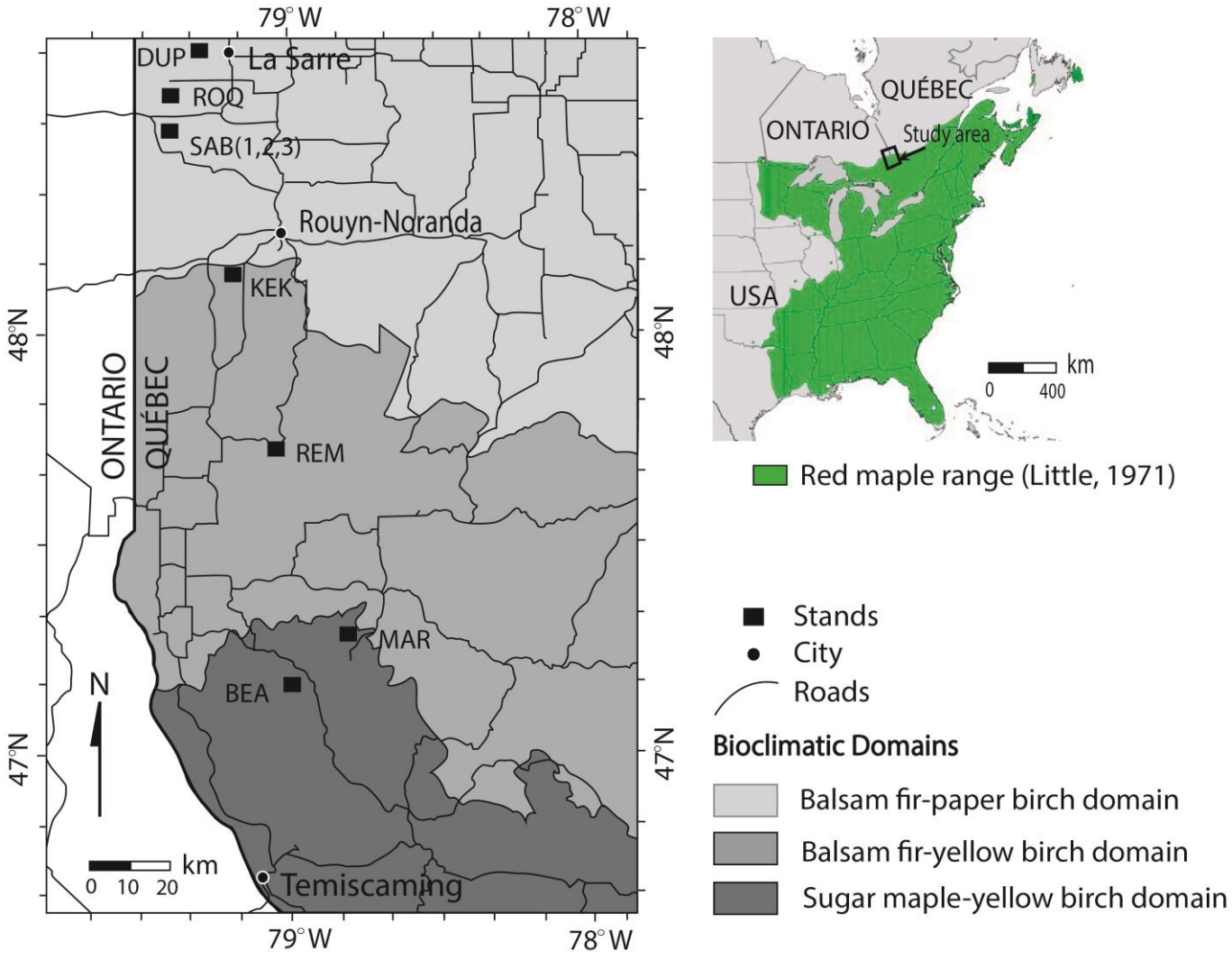
Common interval analysis for 1965-2009									
Express population signal (EPS)	0.91	0.85	0.90	0.88	0.87	0.90	0.86	0.89	0.91
Signal-to-noise ratio	10.57	5.53	9.05	6.6	6.50	8.71	5.99	8.47	10.65
Variance explained by the first PC, %	36.89	29.12	49.02	44.0	44.2	28.93	30.21	36.03	39.01

686

687 Table 2: Multiple linear regression between cumulative BAI over 2000-2009 and site
688 factors. 95% confidence intervals were obtained by bootstrapping of original dataset 1000
689 times and calculating distribution of the *b* coefficients. For the whole model, the R^2 is
690 0.47 with the 95% confidence interval being 0.29-0.56, and *p* is 0.11 (0.05-0.15).
691

Factor	Estimated coefficient, *b*	95 % confidence interval	Std. Error	t value	p value
Intercept	-149.50	-354.30 - -79.40	52.49	-2.85	0.04
Latitude	3.21	1.93 - 22.56	1.09	2.96	0.03
Competition	-2.29	-11.50 - 7.82	2.09	-1.10	0.32
Soil pH	0.63	-3.29 - 7.28	1.48	0.43	0.69

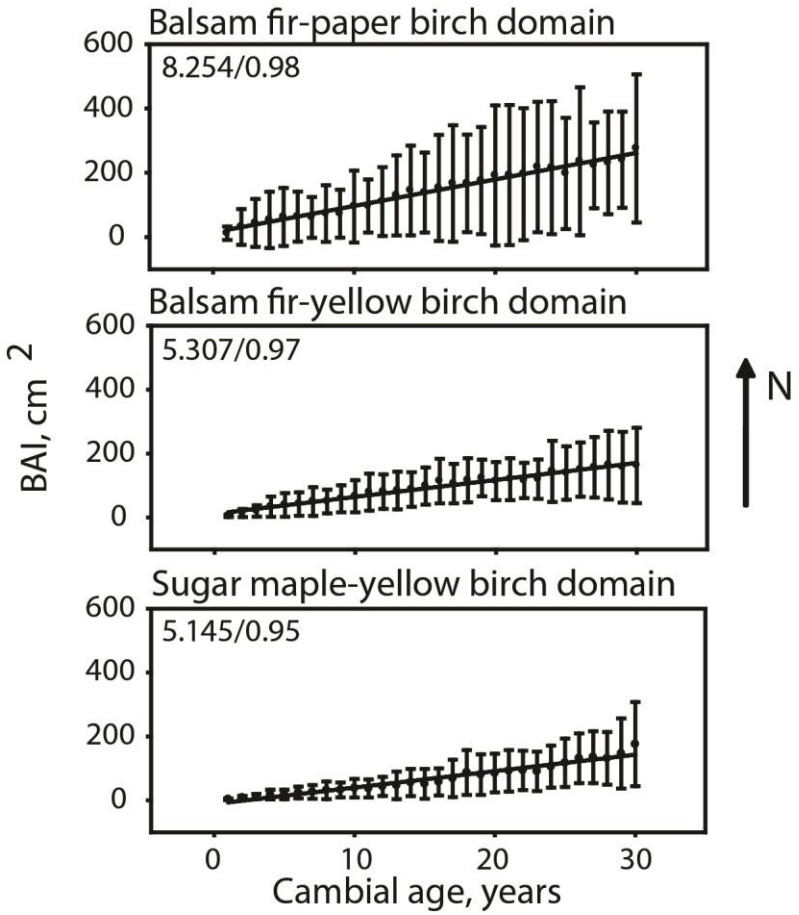
692



693

694 Figure 1: Site locations and distribution range of red maple.

695



696

697 Figure 2: Cambial age BAI chronologies of red maple in the three bioclimatic domains at
698 its northern distribution limit, computed for the first 30 years of tree lifespan. Vertical
699 bars represent SD (standard deviations) for a given cambial age. Data are fitted by linear
700 regression with values of slope coefficient b and r^2 given for each domain.

701

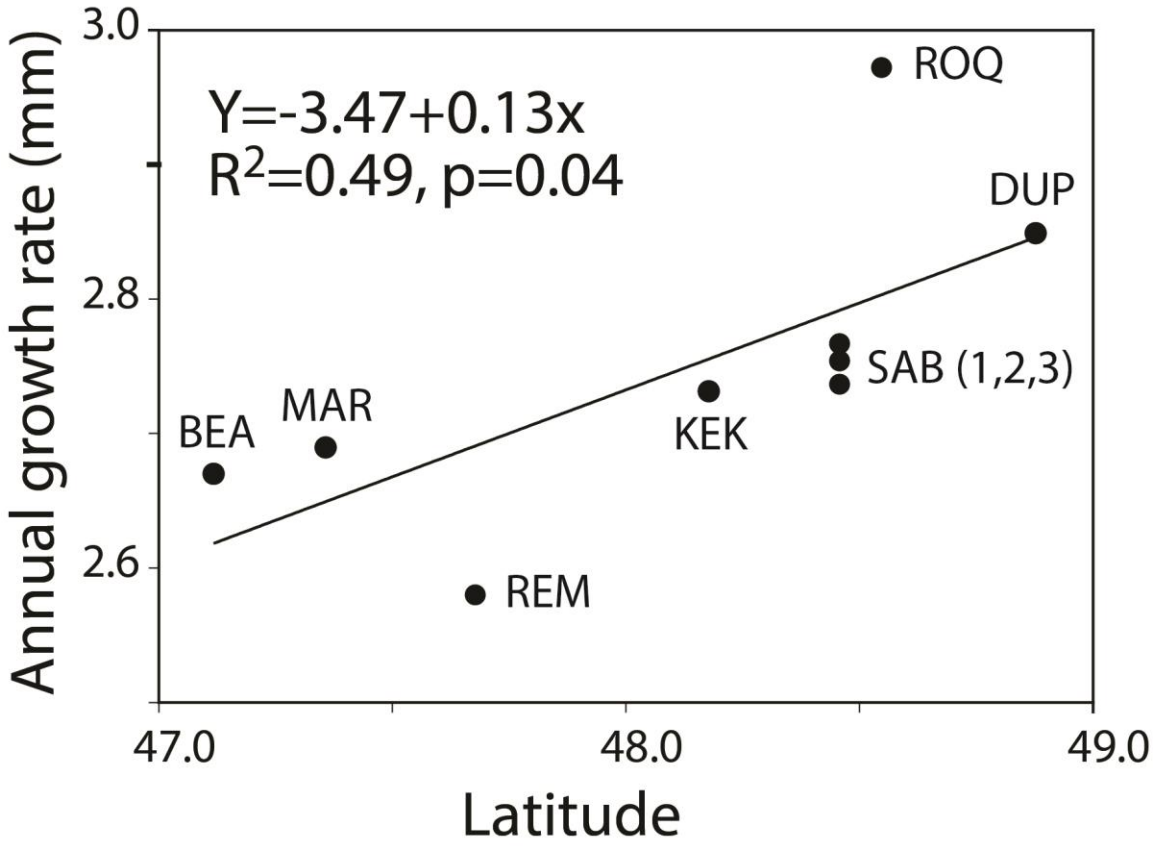
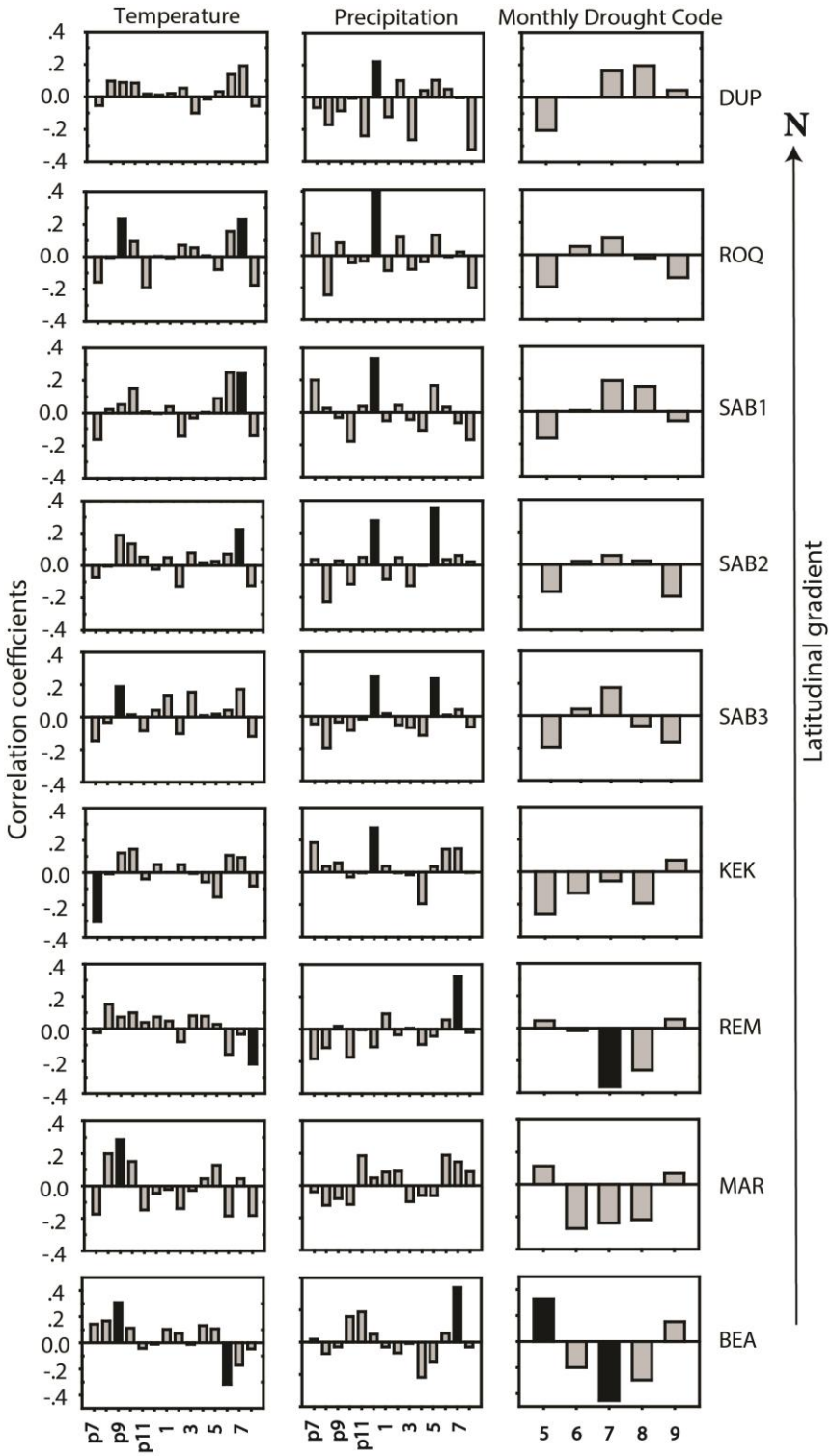


Figure 3: Mean diameter growth rate of whole lifespan along the latitude and linear regression between them.



706

707 Figure 4: Correlation coefficients of response function analyses for red maple from
708 previous year July to current year August for the period 1965-2009 at its northern limit. A
709 black bar indicates a significant relationship at $p = 0.05$.

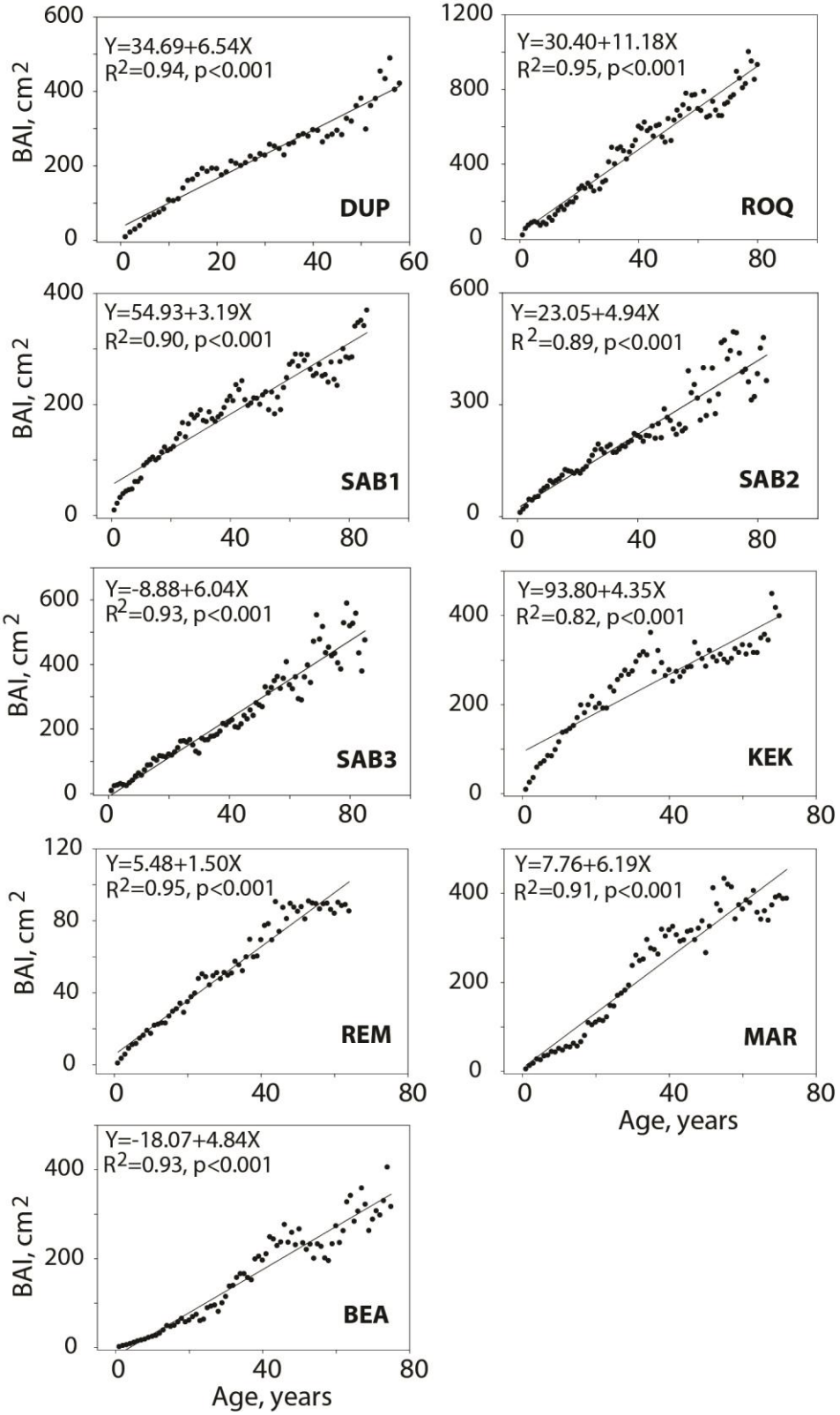
Supplementary Data

Table S1: Soil texture of red maple at the nine sites in western Quebec.

Site	Sand, %	Silt, %	Clay, %	Texture Class
DUP	95.5	1.0	3.5	Sand
ROQ	91.3	6.0	2.7	Sand
SAB1	92.5	4.8	2.8	Sand
SAB2	85.1	9.4	5.5	Sand
SAB3	90.3	7.0	2.7	Sand
KEK	87.5	12.2	0.2	Sand
REM	89.5	4.0	6.5	Sand
MAR	73.3	17.5	9.2	Sandy loam
BEA	95.5	1.5	3.0	Sand

714 Table S2: Soil chemical component of red maple at studied sites in western Quebec.
715

Sites	C total	N total	S total	pH	P	K	Ca	Mg	Mn	Al	Fe	Na	C.E.C.
	%	%	%	$CaCl_2$	mg/kg	cmol(+)/kg	cmol(+)/kg	cmol(+)/kg	cmol(+)/kg	cmol(+)/kg	cmol(+)/kg	cmol(+)/kg	cmol(+)/kg
DUP	0.92	0.02	<0.01	4.08	10.86	0.06	0.42	0.11	0.02	14.34	2.66	0.03	17.63
ROQ	2.21	0.11	0.02	3.99	8.51	0.08	0.62	0.21	0.09	15.39	1.57	0.03	18.00
SAB1	1.77	0.06	0.01	3.04	16.05	0.06	0.17	0.12	0.00	4.88	0.60	0.03	5.86
SAB2	6.50	0.30	0.04	3.51	28.92	0.19	0.57	0.28	0.03	15.89	2.65	0.04	19.65
SAB3	6.38	0.34	0.06	3.87	13.05	0.18	0.28	0.21	0.02	19.51	2.14	0.04	22.39
KEK	8.15	0.45	<0.01	3.92	7.77	0.24	0.78	0.36	0.17	20.58	1.60	0.06	23.79
REM	3.53	0.18	0.04	3.82	2.84	0.10	0.73	0.36	0.01	18.15	2.11	0.03	21.51
MAR	3.82	0.21	0.03	4.01	23.35	0.16	0.78	0.33	0.05	17.08	2.22	0.06	20.69
BEA	1.50	0.05	0.01	4.20	161.73	0.17	1.49	0.48	0.11	15.00	3.01	0.03	20.30



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717 Figure S1 Averaged linear BAI trend at nine sites over the entire tree lifespan.